

ANTENNARIA PULVINATA GREENE: THE
LEGITIMATE NAME FOR *A. AROMATICA* EVERT
(ASTERACEAE: INULEAE)

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ABSTRACT

Canonical variates analysis was used as an analytical technique to document morphological discontinuities among individuals of *Antennaria media* ($n = 63$), *A. pulvinata* ($n = 103$), *A. rosea* ($n = 64$) and *A. umbrinella* ($n = 65$). Evaluation of the defined classification criterion indicated that 94% of the specimens were classified correctly. The classification criterion was subsequently used to classify type collections of *A. aromatica* ($n = 26$) into one of the previously defined groups. Results based on these analyses as well as previously published information demonstrate that *A. aromatica* and *A. pulvinata* are morphologically indistinguishable. The analyses also indicate that *A. pulvinata* and *A. rosea* exhibit morphological integrity relative to each other and would best be treated as distinct species. The four species, *A. media*, *A. pulvinata*, *A. rosea* and *A. umbrinella*, exhibit morphological integrity and should be treated as distinct. A list of synonymy is provided for *A. pulvinata*.

Key Words: *Antennaria media*, *A. pulvinata*, *A. rosea*, *A. umbrinella*, *A. aromatica*

INTRODUCTION

Antennaria aromatica Evert was originally described as a sexual diploid Cordilleran species (Evert, 1984). Subsequent studies have demonstrated that the species is morphologically, cytologically and reproductively more variable (Bayer and Stebbins, 1987; Bayer, 1984, 1989a), as well as more widely distributed (Chmielewski and Chinnappa, 1988a; Bayer, 1989a), than initially proposed. Additional interest in *A. aromatica* stems from the implication that the species is one of the progenitors of the *A. rosea* Greene polyploid complex, specifically, that entity described as *A. rosea* subsp. *pulvinata* (Greene) R. Bayer (Bayer, 1989b).

Evert (1984) was able to differentiate *Antennaria aromatica* from both *A. media* Greene and *A. umbrinella* Rydberg, other members of the complex, by its copious and persistent glandulosity, widely cuneate-spatulate basal leaves and distinctive citronella-like odor. Bayer (1989b) concluded that his subsp. *pulvinata* resembled *A. aromatica*, except in that it lacked glandular hairs. Although Greene (1898) described both "female" and "male" specimens of *A. pulvinata*, Bayer (1989b) concluded that his subsp. *pulvinata* is entirely pistillate, apomictic and polyploid.

Antennaria aromatica was initially considered endemic to southwestern Montana and adjacent parts of Idaho and Wyoming occupying limestone talus and xeric habitats (Evert, 1984). The species was subsequently reported from Alberta, British Columbia and California (Chmielewski and Chinnappa, 1988a). Bayer (1991) rejected the latter range extension, citing specimen misidentification, as determined by either inspection or deduction, and instead supported the distribution for the species presented by Bayer (1989a).

Although *Antennaria aromatica* was originally described as an endemic, morphologically uniform, sexual diploid species, five years later it was more appropriate to consider the species as wider ranging (Chmielewski and Chinnappa, 1988a; Bayer 1989a), reproductively variable (either sexual or apomictic) and cytologically variable (diploid, tetraploid or hexaploid) (Bayer and Stebbins, 1987; Bayer 1989a). Reproductive biology, hybridization, polyploidization and dioecism have all contributed to morphological intergradation among species of *Antennaria* and thereby magnified the present state of confusion not only in this species but also the genus (Fernald, 1950; Cronquist, 1955; Anderson, 1959; Hultén, 1968; Welsh, 1974; Scoggan, 1979; Porsild and Cody, 1980; Moss, 1983).

This investigation incorporates the results of a phenetic study of gross morphology with information published during the past decade to determine whether it is possible to distinguish consistently and confidently among *Antennaria aromatica*, *A. media*, *A. pulvinata* (including subsp. *albescens* E. Nelson), *A. rosea* and *A. umbrinella*. Having established those taxa which are distinct, some comments are offered concerning the presumed evolutionary history of the group.

MATERIALS AND METHODS

Herbarium specimens, including type material, utilized in the phenetic study were borrowed from ALTA, ARIZ, CAN, COLO, DAO, F, LEA, MO, MONT, MOR, MT, NY, OS, PH, RM, SLRO, UAC, UBC, UC, US, WIN and ws (Holmgren et al., 1990). Specimens of each species were selected on the basis of completeness and comparability in terms of developmental stage. Only mature pre-dehiscent specimens were included. These specimens reflect a range in plant size,

Table 1. Morphological characters included in the phenetic study of *Antennaria aromatica*, *A. media*, *A. pulvinata*, *A. rosea* and *A. umbrinella*.

Structure	Character
Vegetative	Basal leaf length (mm): BASALLL Basal leaf width (mm): BASALLW
Vegetative-Reproductive	Plant height (mm): HEIGHT Number of cauline leaves: NOCAULL Cauline leaf length (mm): CAULLL Cauline leaf width (mm): CAULLW Number of capitula: NOCAP Involucre height (mm): INVOHT Outer phyllary length (mm): OUTPHYL Outer phyllary width (mm): OUTPHYW Inner phyllary length (mm): INNPHYL Inner phyllary width (mm): INNPHYW
Reproductive	Pappus length (mm): PAPPUSL Corolla length (mm): COROLLAL

involucre size, habit and provenance. No *a priori* restrictions were placed on the total number of specimens considered necessary to represent the range of morpho-geographic variation within each species. Herbarium specimens ($n = 295$) were identified prior to analysis as *Antennaria aromatica* ($n = 26$ type sheets), *A. media* ($n = 63$), *A. pulvinata* ($n = 103$), *A. rosea* ($n = 64$) and *A. umbrinella* ($n = 65$). Qualitative characters used to identify the specimens to species prior to analysis included habit, degree of pubescence, color, shape and texture of the phyllaries, exertion of the style and the presence or absence of papillae on the achenes. These characters were not utilized in the phenetic study. Both pistillate and staminate plants were included in the phenetic study.

Data were collected for 14 quantitative characters for each specimen (Table 1). These characters were selected primarily because they were uncorrelated ($|r| < .70$), described the general form of vegetative and reproductive structures, were not used directly in the classification of individuals to *a priori* groups, were not ipsative and were previously shown to be useful in differentiating among species of *Antennaria* (Chmielewski and Chinnappa, 1988b, 1991; Chmielewski et al., 1990a, 1990b). Several of these characters, including plant height, leaf shape, number of capitula, size of capitula and floret size, are typically used to differentiate among species of *Antennaria*. The data matrix contained no missing values.

Canonical variates analysis was facilitated with the SAS (SAS Institute Inc., 1989) DISCRIM (crossvalidate and posterr options) and CANDISC procedures. To meet the assumptions of multivariate normality (Gilbert, 1968), length measurements were transformed to their logarithms (base 10) and count data were transformed to their square roots prior to initiating multivariate analysis. Classificatory discriminant analysis was used to classify specimens of *Antennaria media*, *A. pulvinata*, *A. rosea* and *A. umbrinella*, defined *a priori* on one or more characters that were not included in the analysis, to species. Correct classification rates and Geisser assignment probabilities were used as indicators of separation among the groups. Tests for equality of group centroids were performed as part of the canonical analysis. The same data set was used to both define and evaluate the classification criterion. The classification criterion was subsequently used to classify the type collections of *A. aromatica* ($n = 26$) into one of the previously defined species. *Antennaria aromatica* was not treated as a separate *a priori* group in the discriminant analysis because the importance of glandularity in the separation of *A. rosea* subsp. *pulvinata* from *A. aromatica* was in my estimation overemphasized. The copious glandularity that is evident on the holotype is less pronounced to lacking on some of the other type collections. Additionally, some specimens that superficially appear non-glandular do possess glands beneath the tomentum. Thus, *A. aromatica* is not considered to be consistently glandular. Trivariate plots of the canonical variate scores were used to facilitate visualization of the results of the multidimensional analysis (DeltaPoint Inc., 1992). Mean value \pm standard deviation was determined for each character for each species.

RESULTS

Canonical variates analysis (CVA) of 14 quantitative morphological characters was used to document discontinuities among specimens of *Antennaria media*, *A. pulvinata*, *A. rosea* and *A. umbrinella*. Evaluation of the classification criterion indicated that 94% of the specimens were classified correctly (Table 2). Geisser assignment probabilities were generally greater than .98 for the 278 correctly assigned specimens. The low error count, in conjunction with the high Geisser assignment probabilities, in-

Table 2. Classification summary by number of observations and percent classified into species for the discriminant analysis.

From Species	Number of Observations and Percent Classified into Species			
	<i>media</i>	<i>pulvinata</i>	<i>rosea</i>	<i>umbrinella</i>
<i>media</i>	54 85.71	8 12.70	0 .00	1 1.59
<i>pulvinata</i>	6 5.83	97 94.17	0 .00	0 .00
<i>rosea</i>	1 1.56	0 .00	63 98.44	0 .00
<i>umbrinella</i>	0 .00	1 1.54	0 .00	64 98.46

dicates that classification of additional specimens, that is, type collections of *A. aromatica*, through the use of the classification criterion, would yield acceptable results.

The first and second discriminant functions accounted for 90.5% (73.1 and 17.4% respectively) of the total variation (eigenvalues of 4.263 and 1.015 respectively) among specimens. Ordination of the 295 specimens by canonical analysis is presented as a series of trivariate plots (Figure 1) in which mean canonical scores are indicated for each species. The Mahalanobis distance between groups and associated F-value indicate the group centroids were significantly different ($P < .0001$). The canonical correlation of the first discriminant function (.900), or that squared as the proportion of the variance in the function explained by the four groups (.810), indicates high to moderate correlation with the groups. A strong relationship between the specific linear combination of variables, the canonical variables and the groups is indicated.

Descriptive statistics (mean \pm standard deviation) are used to identify character discontinuities for the predefined groupings of specimens (Table 3). Except for STEMHT, NOCAULL, CAULLL, BASALLL, NOCAP and INNPHYW which exhibited moderate to no overlap among all or some of the groups, the remaining characters consistently intergraded among the groups. These characters had the highest loadings on the first canonical axis.

Type specimens of *Antennaria aromatica* were classified, through the use of the classification criterion, to either *A. media* (7%, $n =$

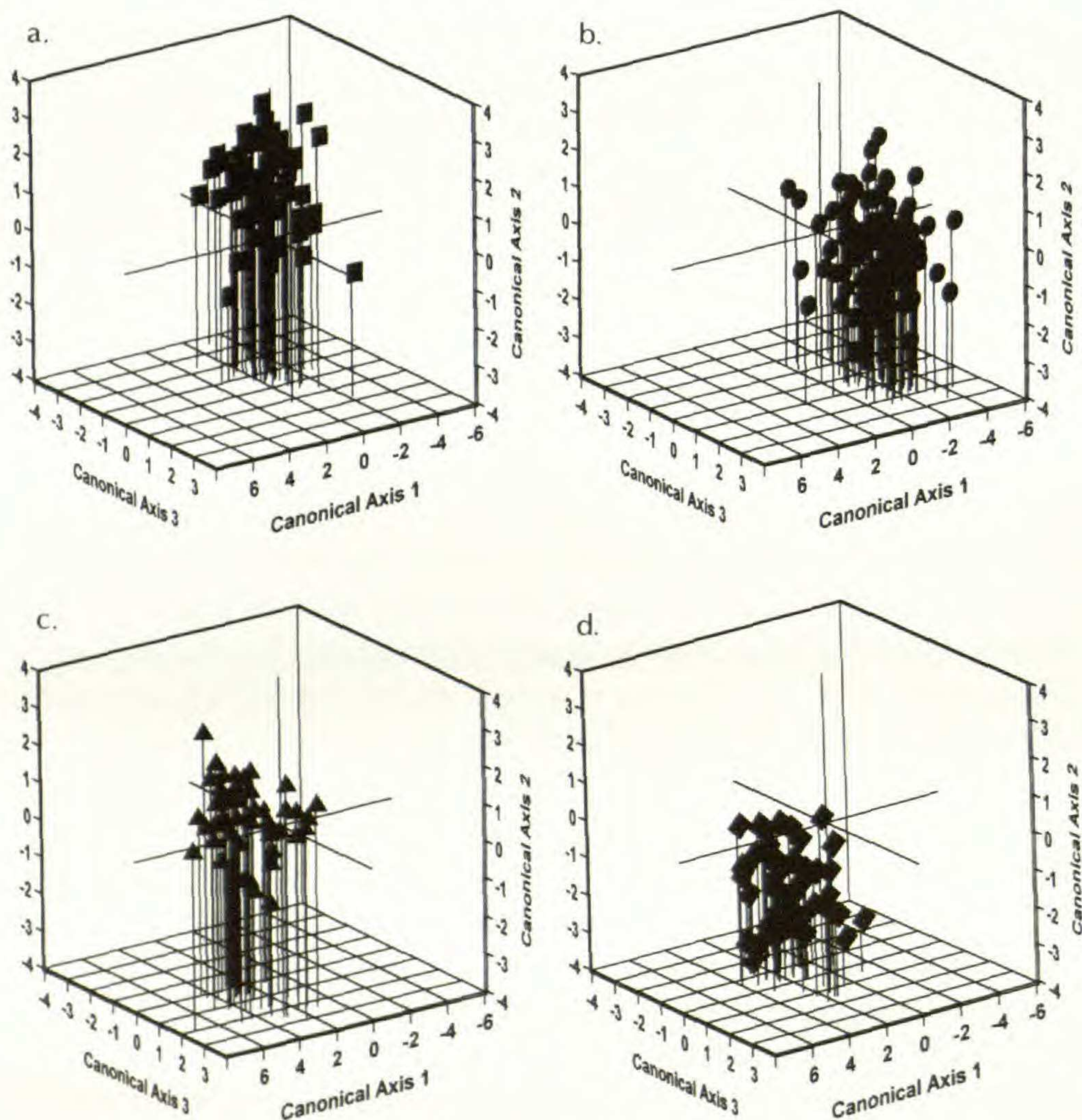


Figure 1. Ordination of a. *Antennaria media* (-.818, 1.277, -1.017); b. *A. pulvinata* (-2.238, -.302, .564); c. *A. rosea* (2.908, .754, .750); and d. *A. umbrinella* (1.476, -1.502, -.646). Group centroids are shown in parentheses (canonical axes 1, 2 and 3 respectively).

2) or *A. pulvinata* (92%, $n = 24$). Geisser assignment probabilities were typically greater than .95 for these specimens.

DISCUSSION

In describing *Antennaria aromatica*, Evert (1984) noted that the species was morphologically uniform throughout its range. Subsequent comparison of the holotype to average species values via a mean similarity matrix employing Pearson product-moment correlation coefficients (see Bayer, 1988a, Table 1) indicated that

Table 3. Summary of mean value \pm standard deviation for each of the taxa included in the phenetic study.

Character	Taxon				
	<i>aromatica</i>	<i>media</i>	<i>pulvinata</i>	<i>rosea</i>	<i>umbrinella</i>
STEMHT (cm)	3.12 \pm 1.46	5.98 \pm 2.63	5.11 \pm 2.61	19.81 \pm 8.55	10.26 \pm 3.95
NOCAULL	5.42 \pm 1.68	6.65 \pm 1.99	6.56 \pm 1.82	12.25 \pm 3.31	8.49 \pm 2.09
CAULLL (mm)	8.23 \pm 2.23	11.43 \pm 3.18	9.93 \pm 2.48	21.18 \pm 6.26	11.96 \pm 2.91
CAULLW (mm)	1.87 \pm 0.63	1.71 \pm 0.52	1.80 \pm 0.48	2.25 \pm 0.84	1.82 \pm 0.53
BASALLL (mm)	8.25 \pm 2.04	12.07 \pm 3.62	8.72 \pm 2.89	17.13 \pm 5.40	10.31 \pm 3.18
BASALLW (mm)	4.28 \pm 1.20	3.33 \pm 0.96	4.15 \pm 1.16	3.98 \pm 1.29	3.49 \pm 0.83
NOCAP	3.42 \pm 0.99	5.00 \pm 1.49	4.44 \pm 1.31	12.16 \pm 7.79	8.20 \pm 3.27
INVOHT (mm)	5.32 \pm 0.79	5.58 \pm 0.66	5.93 \pm 0.85	5.68 \pm 0.71	4.78 \pm 0.73
OOUTPHYW (mm)	3.74 \pm 0.79	3.90 \pm 0.64	4.04 \pm 0.68	3.81 \pm 0.64	3.28 \pm 0.54
OINPHYW (mm)	1.20 \pm 0.21	1.23 \pm 0.24	1.38 \pm 0.25	1.09 \pm 0.23	1.05 \pm 0.20
ININPHYW (mm)	4.87 \pm 0.74	5.08 \pm 0.61	5.35 \pm 0.68	5.07 \pm 0.65	4.15 \pm 0.62
ININPHYW (mm)	1.03 \pm 0.33	0.77 \pm 0.21	0.90 \pm 0.24	0.48 \pm 0.17	0.64 \pm 0.24
PAPPUSL (mm)	3.86 \pm 0.81	4.73 \pm 0.63	4.57 \pm 0.72	4.43 \pm 0.59	3.66 \pm 0.52
COROLLAL (mm)	3.54 \pm 0.51	3.57 \pm 0.57	3.83 \pm 0.64	3.40 \pm 0.51	2.80 \pm 0.53

it is "atypical of the species, consisting of really small diploids that do not occur on limestone talus" (Bayer, pers. comm. 1989). Examination of available type material ($n = 26$) indicated that *A. aromatica*, like most *Antennaria* (Chmielewski and Chinnappa, 1988b, 1991; Chmielewski et al., 1990a, 1990b), is indeed variable, exhibiting different degrees of plasticity, with respect to basal leaf length and width, plant height, cauline leaf length and width, degree of pubescence, glandularity and involucre height. *Antennaria aromatica* is therefore a species which illustrates that the nomenclatural type is not necessarily the most typical or representative element of the taxon; it is merely that element with which the name is permanently associated (Lanjouw et al., 1966).

Initially described as a diploid species (Evert, 1984), *Antennaria aromatica* was subsequently reported to include both tetraploid and hexaploid individuals (Bayer, 1984, 1989a; Bayer and Stebbins, 1987). Apparently some confusion exists with respect to the identification of the tetraploid specimen designated CO-458 (Bayer and Stebbins, 1987), as it was included with both *A. aromatica* (toward *A. media*) and *A. rosea* (toward *A. aromatica*) by the authors. This confusion notwithstanding, it is likely that the diploid and polyploid states possessed by individuals of the species have contributed, at least in part, via the gigas effects of polyploidization (Stebbins, 1971) to the observed patterns of plasticity (see also Bayer, 1989b) noted above. Because so few cytological determinations are available for the species, statistically valid conclusions pertaining to the relationship between chromosome number and morphology are not possible at this time.

Results based on canonical variates analysis indicate that the degree of morphological overlap among the four taxa, *Antennaria media*, *A. pulvinata*, *A. rosea* and *A. umbrinella*, as defined in this study, is minimal. High assignment rates and Geisser assignment probabilities support this conclusion. The conclusion that *A. media*, *A. rosea* and *A. umbrinella* are morphologically distinct is not a novel one as the species are generally treated as such (see Bayer, 1988a, 1988b, 1989c, 1990a; Chmielewski and Chinnappa, 1988b; Chmielewski et al., 1990a, 1990b for discussion). The question remains, how does *Antennaria pulvinata* fit in with these species?

Direct visual comparison of type material indicates that fragments of the holotypes of *Antennaria aromatica* (RM346356) and

A. pulvinata (NDG058584) are indistinguishable, as are the paratype of *A. aromatica* (F) and the isotype (CAN105666) and paratype (CAN105674) of *A. pulvinata*.

Although two type collections of *Antennaria aromatica* were originally assigned to *A. media*, through the use of the classification criterion, the 92% success rate observed is in line with the capabilities of the classification criterion as it was defined through the analysis. The classification criterion obtained through canonical variates was initially evaluated at a 94% success rate. Thus, it is unrealistic to expect a higher classification success rate when it is used to classify collections, such as the types of *A. aromatica*, which were not used to define the classification criterion. The analysis demonstrates not only that *A. aromatica* and *A. pulvinata* are indistinguishable but also that morphological intergradation among species of *Antennaria* is a facet of reality.

In attempting to clarify the confusion that surrounds the identity of *Antennaria pulvinata*, Bayer (1989a) concluded that it resembles *A. aromatica* closely, except that it lacks glandular hairs. This character is not infallible however, as glandularity, even among type collections of *A. aromatica*, ranges from a dense cover to trace amounts or even lacking. Additionally, some specimens that superficially appear non-glandular do possess glands beneath the tomentum. Thus *A. aromatica* is not consistently copiously glandular, but rather variable in this regard.

Inasmuch as *Antennaria pulvinata* and *A. aromatica* are identical, the basis for inclusion of the former in *A. rosea* is elusive. If *A. pulvinata* should be included at some taxonomic rank in the *A. rosea* polyploid complex, as proposed by Bayer (1989b), then the results of canonical variates analysis should support this contention. Support would include lower assignment rates for both taxa, as well as lowered Geisser assignment probabilities. Neither of these scenarios is true however in the present study. In circumscribing *A. rosea*, Bayer (1989b) concluded that subsp. *pulvinata* is entirely pistillate, apomictic and polyploid. This non sequitur is unacceptable however as Greene (1898) described both "female" and "male" specimens of *A. pulvinata*. The protologues of *A. pulvinata* and *A. rosea*, gross morphology of type material and the results of canonical variates analysis, all contribute to support the conclusion that the two taxa are morphologically distinct. The two taxa, *A. pulvinata* and *A. rosea*, do exhibit mor-

phological integrity (see Table 3) and should therefore be treated as distinct. As such, it would be inappropriate to include the former species as an infraspecific subdivision of the latter.

Although originally described as an endemic, morphologically uniform, sexual, diploid species, *Antennaria aromatica* is more appropriately described as wider ranging (Chmielewski and Chinappa, 1988a; Bayer, 1991), both sexual and apomictic (Bayer, 1989a), diploid and polyploid (Bayer, 1989a) and morphologically variable. Gross morphology of type and non-type material, the Pearson product-moment correlation coefficients presented by Bayer (1988a), the protologues of *A. aromatica* and *A. pulvinata*, the fallibility of using glandularity as a diagnostic character and the results of canonical variates analysis all contribute, to varying degrees, to support the conclusion that *A. aromatica* and *A. pulvinata* are conspecific. The latter specific epithet is deemed the legitimate name for the plant and the former a synonym. A list of synonymy is provided for *A. pulvinata*.

TAXONOMY

The following key may be used to differentiate among the *Antennaria media*, *A. pulvinata*, *A. rosea* and *A. umbrinella*.

- A. Plants generally tall, greater than 1 dm, typically 1.5–2.5 dm; cauline leaves long, 1.5+ cm, numerous; basal leaves typically lanceolate, occasionally spatulate-lanceolate, 1.2+ cm long; immature involucre nodding *A. rosea*
- A. Plants generally compact, less than 1 dm, typically 0.5–1.0 dm; cauline leaves shorter, <1.5 cm, fewer; basal leaves spatulate, obovate, spatulate-obovate, cuneate spatulate to occasionally oblanceolate, typically <1.2 cm; immature involucre not nodding B
- B. Stolons elongate, strongly upsurgent at tips and usually woody; basal leaves tufted about stem; tips of involucral bracts dirty white or light brown *A. umbrinella*
- B. Stolons short, not upsurgent; basal leaves not tufted about stem; tips of involucral bracts conspicuously darker than base, brown, green, black C
- C. Basal leaves typically spatulate-lanceolate with permanent woolly tomentum; inner bracts narrow, linear, tips usually sharp pointed, acute . . . *A. media*

- C. Basal leaves widely cuneate-spatulate to occasionally oblanceolate; persistently white tomentose on both surfaces; inner bracts broader, frequently obtuse . . .
 *A. pulvinata*

LIST OF SYNONYMY

- Antennaria pulvinata* Greene, Pittonia 3: 287, 1898. TYPE: Canada: Alberta, Moose Mtn, Elbow River, Rocky Mountains, June 29, 1897, *J. Macoun 18491*. (HOLOTYPE: NDG058584!; ISOTYPE: CAN105666!). *J. Macoun 18493, 18495, 18498*. (PARATYPES: CAN105675!, CAN105674!, NDG058583!, NDG058584!). *J. Macoun 18492*. (TOPOTYPE: CAN105676!).
- Antennaria rosea* subsp. *pulvinata* (Greene) R. Bayer, Brittonia 41: 59, 1989.
- Antennaria pulvinata* subsp. *albescens* E. Nelson, Proc. U.S. Natl. Mus. 23: 702, 1901. *Antennaria albescens* (E. Nelson) Rydb. Rocky Mts. 917, 1067, 1917. TYPE: United States: Idaho, Texas District, Mount Hops, Salmon River Mountains, Aug 17, 1895, *L. F. Henderson 3870*. (HOLOTYPE: US228762!).
- Antennaria aromatica* Evert, Madroño 31: 109, 1984. TYPE: United States: Montana, Carbon Co., Beartooth Range along Hwy 212, ca. .8 km N of Quad Cr., Aug 5, 1981, *E. F. Evert 3406*. (HOLOTYPE: RM346356!; ISOTYPES: MO3229695!, MOR52039!, UC1509580!). *F. W. Pennell, F. B. Cotner and R. L. Schaeffer 23835*. (PARATYPES: F1576300!, PH853371!). *R. J. Bayer and G. L. Stebbins 8092*. (PARATYPE: OS153623!). *E. F. Evert 1780, 3015, 3420*. (PARATYPES: RM346360!, RM346359!, RM346357). *P. A. Robertson 1110*. (PARATYPE: RM330754!). *G. L. Stebbins and R. J. Bayer 8113*. (PARATYPE: UAC41448!).

The original species description of *Antennaria pulvinata* (Greene, 1898), supplemented by the species description for *A. aromatica* (Evert, 1984), deemphasizing glandularity as a diagnostic character for the latter, adequately reflects the morphology of the former as it was applied at the completion of this study. Species descriptions previously presented for *A. media* (including *A. pulchella* Greene, Bayer, 1990b), *A. rosea* (Chmielewski et al., 1990a) and *A. umbrinella* (Chmielewski et al., 1990a) are deemed accurate and were applied accordingly in this study.

The distributions presented for *Antennaria media* (Bayer, 1990b), *A. pulvinata* (as discussed for *A. aromatica* in Chmielewski and Chinnappa, 1988a), *A. rosea* (Chmielewski and Chinnappa, 1988b) and *A. umbrinella* (Chmielewski et al., 1990a) are considered to accurately represent the ranges of these species as they are presently understood.

EVOLUTIONARY RELATIONSHIPS

Antennaria media sensu lato, considered by some to be one of the more important western species of *Antennaria* (see Bayer, 1987a), has been implicated in the hybridization events which resulted in *A. alpina* (L.) Gaertner, *A. parvifolia* Nuttall and *A. rosea*. Additionally, *A. media* is considered to possess a pivotal genome, being partially responsible for *A. parlinii* Fernald overlapping morphologically with *A. neodioica* Greene; *A. neodioica* with *A. parvifolia*; *A. parvifolia* with *A. rosea*; and *A. rosea* with *A. alpina* (Bayer, 1987a). The importance of *A. media* in the evolution of all these taxa is in my estimation overemphasized as these apparent relationships represent speculation based on little or no data.

A recent revision of *Antennaria media sensu lato* led Bayer (1990b) to conclude that the diploid cytotype (*A. pulchella* Greene) should be recognized as distinct from the polyploid cytotypes represented by *A. media*. This conclusion, founded on the results of a phenetic study, warrants discussion. First, although polyploid *A. media* occurs throughout the alpine zone of many western North American mountain ranges, extending from the southwestern United States to the western arctic, only specimens from the southern portion of its distribution were included in the analysis. Second, the data set utilized was incomplete and therefore subject to produce unsupported results (see Chmielewski and Chinnappa, 1992). Third, except for *A. scabra* Greene, the taxa included in the list of synonymy were not utilized in the analysis. Fourth, many additional taxa which were previously included in the complex were excluded without comment from the phenetic study (*A. atriceps* Fernald ex Raup, *A. compacta* Malte, *A. fusca* E. Nelson, *A. maculata* Greene, *A. modesta* Greene, *A. mucronata* E. Nelson, *A. pallida* E. Nelson and *A. stolonifera* A. E. Porsild). Additional taxa which I believe should be considered in a revision of *A. media sensu lato*, but which were placed in synonymy with *A. rosea* (Bayer, 1989b), include *A. chlorantha* Greene, *A. lanulosa* Greene, *A. isolepis* Greene and *A. tomentella* E. Nelson. Fifth, although *A. scabra* was considered most similar to *A. aromatica* based on the results of an average similarity matrix (Bayer, 1988a), Bayer (1990b) failed to address this discrepancy, concluding that it was most similar to *A. pulchella*. Similar discrepancies based on the results of an average similarity matrix (Bayer, 1988a) exist

for *A. austromontana* E. Nelson (most similar to *A. aromatica*), *A. candida* Greene (most similar to *A. umbrinella*) and *A. modesta* (most similar to *A. aromatica*). A phenetic study which includes specimens from throughout the range of *A. media sensu lato* and also incorporates all those taxa which may be part of the complex is necessary before a classification scheme may be legitimately proposed. For the time being it would be prudent to treat these dark green-black phyllaried taxa as members of *A. media sensu lato*.

Bayer (1987b) postulated that *Antennaria rosea* is a polyploid compilospecies, the result of multiple hybridizations among several amphimictic species. Results based on phenetic analyses indicated that *A. aromatica*, *A. corymbosa* E. Nelson, *A. media*, *A. microphylla* Rydberg and *A. umbrinella* are the major sexual progenitors of the complex, whereas *A. marginata* Greene and *A. rosulata* Rydberg are minor contributors (Bayer, 1990a). Chmielewski et al. (1990a) questioned the likelihood of such a complicated pattern of hybridization events across sectional boundaries. The latter authors instead stated that phenetic analyses, based on a substantially larger sample of specimens, supported a hybrid origin among *A. corymbosa*, *A. microphylla* and *A. umbrinella*. Although phenetic analyses have led the aforementioned authors to support different positions relative to the origins of *A. rosea*, isozyme data can be used as independent evidence to support the hypothesis of Chmielewski et al. (1990a), that is, that only *A. corymbosa*, *A. microphylla* and *A. umbrinella* are among the sexual progenitors of the complex (Bayer, 1989d).

Antennaria umbrinella, a member of section *Alpinae* (Chmielewski et al., 1990c) was recently referred to as a member of section *Dioicae* (Bayer, 1987b), as well as section *Alpinae* (Bayer, 1989c). A sexual species, *A. umbrinella* is most similar to *A. pulvinata*, the strongly upsurgent, typically woody stolon tips representative of the former species accounting for morphological divergence between the taxa. The role of this species as one of the progenitors of the *A. rosea* polyploid complex was adequately discussed previously.

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